Estimating mortality rates by capture-recapture, catch-effort and change-in-ratio models for a spring American lobster (*Homarus americanus*) fishery (LFA 23)

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ABSTRACT

Comeau, M., and M. Mallet. 2001. Estimating mortality rates by capture-recapture, catch-effort and change-in-ratio models for a spring American lobster (*Homarus americanus*) fishery (LFA 23). Can. Tech. Rep. Fish. Aquat. Sci. 2373: 20 p.

Mortality rates were estimated for a spring American lobster (*Homarus americanus*) fishery from a single port in the Lobster Fishing Area 23 (southern Gulf of St. Lawrence). Fishery based data were used to calculate catch-effort and change-in-ratio estimates, while data from a single and a double release of tagged lobsters were used in capture-recapture models. Simulations were also done to assess strengths and weaknesses of the various estimators. From the results, none of the proposed estimators can adequately estimate the natural mortality (M). Exploitation rate (u) estimated from three methods ranged between 32% and 83%. However, it is not possible to suggest the "best" value for u since estimators behaved differently under specific simulated conditions. Results from the simulations show that variation in catchability introduces a large bias for fishery based estimators but not for tagging methods. Conversely, the natural mortality does greatly influence u obtained from tagging methods but not the one estimated from fishery based estimators. Furthermore, the recapture rate observed for tagged animals initially captured by traps (32%-37%) was lower than the one for animals initially captured by SCUBA (53%). This is may be cause by a trap-shy response (e.g., the probability of capturing marked individuals is less than the probability of capturing unmarked individuals). This bias could be avoided by using a method different from the fishery for initial capture.

Keywords: American lobster, *Homarus americanus*, Exploitation rate, mortality rate, Capture-recapture, Catch-effort models, change-in-ratio model.

RÉSUMÉ

Comeau, M., and M. Mallet. 2001. Estimating mortality rates by capture-recapture, catch-effort and change-in-ratio models for a spring American lobster (*Homarus americanus*) fishery (LFA 23). Can. Tech. Rep. Fish. Aquat. Sci. 2373: 20 p.

Des taux de mortalité pour une pêche printanière du homard (*Homarus americanus*) dans un port de la zone de pêche au homard 23 (sud du Golfe du Saint-Laurent) ont été estimés. Les estimateurs considérés sont ceux découlant des méthodes de capture-effort et de changement de proportions (change-in-ratio) avec des données provenant de la pêcherie de même que des méthodes de capture-recapture utilisant des homards étiquetés. Les forces et faiblesses des estimateurs sont également étudiées à l'aide de simulations. Il ressort qu'aucun des estimateurs proposés peu adéquatement estimer la mortalité naturelle (M). Les trois méthodes d'estimation du taux d'exploitation (u) produisent des valeurs variants entre 32% et 83%. Il n'est pas possible de déterminer la meilleure estimation de u puisque dans les simulations, chaque estimateur se comportait différemment selon les situations considérées. Une variation dans la capturabilité biaise considérablement les estimateurs basés sur les données de pêcherie mais pas ceux des méthodes de capture-recapture. Inversement, la présence de mortalité naturelle influence grandement l'estimateur de u par capture-recapture, mais pas ceux provenant des données de la pêcherie. De plus, le taux de recapture des individus marqués qui ont été initialement capturés par des casiers (32%-37%) était plus bas que celui des individus initialement capturés par SCUBA (53%). Cette différence est peut-être due à une modification de comportement suite à une première capture, la probabilité de capture des homards étiquetés étant moindre que celle des homards non-étiquetés (trap-shy). Ce comportement pourrait être évité en utilisant une méthode autre que les casiers lors de la capture initiale pour l'étiquetage.

Mots clés: Homard, *Homarus americanus*, Taux d'exploitation, Taux de mortalité, Capture-recapture, Modèle de capture et d'effort, Modèle "change-in-ratio".

1.0. INTRODUCTION

The American lobster (*Homarus americanus*) is one of the most important harvested species in terms of landed value in eastern Canada. The management of this fishery in the southern Gulf of St. Lawrence (sGSL) is through five Lobster Fishing Areas (LFAs) (Fig. 1). These LFAs are managed by seasons which last at most nine weeks, 1 May to 30 June for spring fisheries (LFAs 23, 24, 26A, 26B), and 10 August to 10 October for the fall fishery (LFA 25).

Assessment of the lobster fisheries could be difficult as LFAs were created for management purposes, and do not necessarily represent biological units. For instance, LFA 23 consists of fishing grounds located in Baie des Chaleurs and in the sGSL, two highly different marine environments with specific fishing characteristics such as vessel size, distance between home port and fishing grounds, water depth, and trap type. Although traps are the sole fishing gear permitted in Canada for the lobster fishery, their size and construction material (wood, wire) vary among fishermen within a wharf, thus complicating the definition of a unit of effort. Traps are also equipped with a selectivity mechanism allowing sub-legal size animals to escape. All of these factors contribute to the difficulties of accurately estimating lobster fishery parameters for an entire LFA as most methods proposed assume constant catchability, constant natural and fishing mortality within a season, and no migration of the population.

In the sGSL, landings have increased from the record low observed in 1974 to the record high in early 1990's, since then, there is a slow but steady decline (Lanteigne and Mallet, 1995). The declining trend in lobster landings was observed for the entire Canadian Atlantic coast, and prompted the formation of a committee under the Fishery Resource Conservation Council (FRCC) to review the current approaches to conservation for all the lobster fisheries. The FRCC used an egg-per-recruit (E/R) model (Fogarty and Idoine, 1988) as a reference guide to assess egg production, and presented an extensive overview of values for the entire lobster fisheries on the Canadian Atlantic coast (Anonymous, 1995). In its report, the FRCC concluded that the exploitation rate was too high, and the key elements to achieve a healthy fishery were "good egg production, a reasonable fishing mortality, and a biomass composed of several year classes" (Anonymous, 1995).

The exploitation rate (u) is an important parameter of the E/R model, and in Canada it is estimated using fishery data or tagging studies since there are no fishery independent surveys. Several methods, including length cohort analysis and catch-effort methods (Ricker, 1975; Fogarty, 1995; Cadrin and Estrella, 1996), have been used in the past (Anonymous, 1996a, b, c, and d) to estimate u for all the LFAs within the Maritime Provinces (Table 1). However, since different methods were used for different LFAs, comparison between LFAs (LFA 23 to 34) is difficult. Furthermore, most of these methods have never been compared for their accuracy and validity for lobster, although Miller and Mohn (1993) indicated that the Leslie analysis, an analysis of catch-effort data, is not recommended for lobster fisheries since most of the assumptions are violated.

Another approach that has not been used until now, and could be considered for the American lobster, is the change-in-ratio (CIR). Frusher et al. (1997) successfully used this approach to estimate u for the Tasmanian rock lobster (*Jasus edwardsii*) fishery. This method is based on the proportions of legal size and sub-legal animals captured at the beginning and the end of the fishing season.

Mark-recapture studies mostly based on the Petersen model (Ricker, 1975) were also used to estimate u, and the instantaneous natural mortality rate (M). In one of the first attempts to estimate u based on tagging, Paloheimo (1963) reported that tag returns were influenced by water temperature and the number of days lobsters were at large in the sea. Another trial was carried out to estimate u based on a tagging project by Ennis et al. (1982) in Comfort Cove Newfoundland. Both authors used the Petersen model to estimate the size of the lobster population, and derived u. In the United States, Krouse (1981) and Briggs and Mushacke (1984) estimated the instantaneous fishing mortality rate (F) using Gulland's model (Gulland, 1969).

The main objective of this study is to estimate mortality rates by mark-recapture, catch-effort, and CIR models for assessing the spring lobster fishery at Stonehaven New Brunswick located in the Baie des Chaleurs (LFA 23 within the sGSL). The strengths and weaknesses of the models are examined using fishery data collected in 1997, and simulated data sets.

2.0. Materials and methods

2.1. Tagging

Two tagging projects were carried out in Stonehaven located on the south shore of Baie des Chaleurs in New Brunswick, Canada (47°45.2'N:65°21.6'W) (Fig. 1). The first tagging project was carried out after the molting season (July-August) on 10 September 1996, (two months after the 1996 fishing season ended), and the second during the first week of the 1997 fishing season on 5 May (i.e. four days after the start of the season). Tagging before the beginning of the 1997 fishing season was not possible due to heavy ice conditions. A total of 289 and 355 commercial size lobsters ($\geq$ 66.7-mm of carapace length) were captured using commercial traps and tagged in September 1996 and May 1997, respectively. In addition, 36 lobsters captured by SCUBA diving were also tagged and released on 10 September 1996.

All lobsters were tagged inside the lobster holding tanks facility at the Stonehaven wharf with blue streamer tags manufactured by Hallprint PTY.LTD. (27 Jacobsen Crescent, Holden Hill, South Australia, Australia 5088). These tags are made of a thin strip of polyethylene with a narrow band in the middle and a No 6 embroidery needle glued at one end. The tagging technique described by Moriyasu et al. (1995) was used. By using that technique, only the narrow portion of the tag is located inside the animal leaving both ends, with the printed information, visible on the outside. Before their release into the water, tagged lobsters were held in a tank with running seawater for at least 30 min., and any dead or weak lobsters were removed. All lobsters were captured and released on the commercial fishing grounds. Lobsters tagged in September 1996 were released at a single site (depth of 10 m). Lobsters tagged in May 1997 were randomly released over a distance of 5 km on both side of the wharf at depths ranging between 3- and 20-m. Finally, an awareness campaign was conducted to maximize the participation of fishermen in reporting tagged animals as tag recovery took place during the 1997 fishing season. The tag recovery is the most important part of a tagging project to insure the validity of the data to be used in a M-R model (Hearn et al., 1998). When a tagged lobster was captured, the fisherman was requested to bring it to a representative of the tagging project at the wharf. The fisherman was compensated for the market value of the animal. Processing plants returned tagged lobsters not detected by fishermen. None of the recaptured lobsters were returned to the sea.

2.2. Logbook data

Data on landings and trap hauls (effort) for the 1997 fishing season (Table 2) in Stonehaven were obtained through an index-fishermen logbook program, and used to calculate a weekly catch-per-unit-effort (CPUE). Since the 1997 fishing season started on a Saturday, a week was defined as a seven day period starting on Saturday for a total of eight weeks of fishing. A weekly CPUE was found more reliable for assessing the fishery than a daily or three day period CPUE since the lobster catchability is highly variable as it depends on a series of environmental, physiological, and behavioral factors (Krouse, 1989; Comeau and Drinkwater, 1997). There can also be artificial fluctuations in CPUE measured over a three days period especially in the last three weeks of the fishery since fishermen slow down their fishing activity (haul their traps every two days or haul half their traps each day). Logbook data were used in the catch-effort model.

2.3. Size composition

Information on the size (carapace length) and sex of all lobsters captured were obtained during two sessions of sampling at sea (7 May and 18 June 1997) on board a commercial fishing vessel in Stonehaven. A total of six weeks of the fishery elapsed between those sampling sessions. Given that legal size animals are landed, sub-legal animals are returned to the water, and there is no molting during that period, the proportion of legal size lobsters during both sampling periods was used in the CIR model. Berried females, which are protected from harvesting and returned to the water, were not considered in this study.

2.4. Statistical analyses

2.4.1. Tagging studies

Three mark-recapture models were considered, one for a closed population, and two for an open population. Two models are based on a single mark-recapture (M-R) followed by recapture while the third model assumes two mark-releases (M-M-R) with a recapture period following the second release. Recovery periods are known for each tagged individual (Table 2). Underlying assumptions for all tagging studies are:

1. No (or negligible) immigration and emigration out of the study site, and there is no recruitment.
2. Constant F for tagged individuals.
3. No tag lost or tag-induced mortality.
4. Tagged individuals behave independently of each other, i.e. no schooling.
5. Tagged individuals mix with the untagged population.

Further assumptions are required for some models and are given with their definition. Estimates obtained can be applied to the whole population if F and M (for an open population) are assumed similar for the tagged and unmarked population.

2.4.1.1. Single mark-release followed by recapture: closed population: When the release of tagged lobsters is followed by one or many instantaneous samplings, Paloheimo (1963) suggested using the Petersen model for a closed population (Petersen, 1896) to obtain the population size estimate and u. To apply the Petersen model, the above assumptions 1 to 5 must hold as well as the following:

i. There is no natural mortality.
ii. All recaptured animals are reported.

Suppose m tagged individuals are released prior to the fishery, and r tagged individuals are recaptured during the fishery. The u is estimated by the proportion of tag return, that is $\hat{u} = r / m$ (see Ricker (1975) and Seber (1982) for complete equations).

2.4.1.2. Single mark-release followed by recapture: open population: The M-R for an open population model was described by Paulik (1963), and is similar to mortality estimates from M-R models described by Gulland (1955) and Chapman (1961) (see Seber, 1982, p. 271-276). Paulik's method consists of tagging and releasing m individuals prior to the beginning of the fishing season or sampling period. The release is followed by a series of instantaneous random samples permanently removed from the population including r tagged individuals. By analyzing the recapture pattern (time of recapture are recorded), fishery parameters can be estimated. Validation of the method lies upon the assumptions 1 to 5 listed above as well as:

i. For tagged individuals, M is constant.
ii. All tagged animals captured are reported.

Except for variance estimates of total mortality rate (Z) and M, equations used can be found in Seber (1982, p.271-276). Equations used to compute Z, M, F, and u, and their variance, with notation adapted to the fishery research, are presented in Appendix I.

2.4.1.3. Two mark-releases followed by recapture: open population: The M-M-R for an open population model is an extension of the M-R model (Paulik, 1963). It can also be seen as a special case of Ricker's (1958) two-release model. It consists of two successive marking periods followed by a recapture period. All tagged animals captured are permanently removed from the population, thus multiple recapture of the same animal is not possible. Suppose a first tag-release is done some time (τ_1) before the fishing season with m_1 tagged individuals released, and a second tag release of m_2 individuals is done immediately preceding the season ($\tau_2=0$). Fishermen then recapture the individuals during the fishing season. The model relies on the assumptions 1 to 5 listed above as well as:

i. For tagged individuals, M is constant.
ii. All tagged animals have the same probability of being captured in a particular sampling period (given that they are alive at the beginning of the period), irrespective of which tag release they are from.
iii. The pre-season M is the same as the one during the season.
iv. A constant proportion of animals survives the tagging process equally for both tagging periods. It is further assumed that the tagging induced mortality occurs within a short period after tagging.
v. The probability that a recaptured animal is reported remains constant during the entire season for all types of tag.

These assumptions are similar to the M-R model for an open population but this time, non-reporting of tagged animals does not bias the estimators of mortality as long as the non-reporting is unrelated to the release period. For the present study, identical tags were used for both releases, therefore the dependence of non-reporting and the release period is unlikely. Under these assumptions, both tagging studies should have a similar recapture pattern. The estimate of M would then be established by the difference between the proportion of recaptures.

As for the M-R method for an open population, most estimators used are given in Seber (1982, p.287-290). A summary of the equations used to calculated Z, M, F, and u, and their variance is presented in Appendix II.

2.4.2. Catch-effort models

Catch-effort models are based on the assumption that the size of a sample captured from a population is proportional to the fishing effort used to retrieve the sample. Hence, one unit of sampling effort is assumed to catch a fixed proportion of the population. If samples are permanently removed, the decline in population size will produce a decline in CPUE. A baited trap is considered to be a unit of effort. Model assumptions common to both closed and open population are:

I. Sampling is a Poisson process with regard to effort meaning that the probability of a given individual being captured when the population is subjected to f units of sampling effort is qf. The catchability coefficient (q) is assumed to be constant throughout the whole experiment and the same for each individual. Units of effort are assumed to be independent, i.e. traps do not compete with each other.
II. All individuals have the same probability P_j of being captured in the j^{th} sample given they were alive just before the sample. From assumption (I), we have $P_j = 1 - \exp(-qf_j)$.
III. All removals are known.
IV. No migration.

2.4.2.1. Catch-effort model: closed population: Let N represent the initial population size, n_j the size of the j^{th} sample removed from the population (j=1,..., J), f_j the units of effort expended on the j^{th} sample. To the above assumptions I to IV, the catch-effort model also requires that:

i. The population is closed, and that there is no mortality or recruitment during sampling (fishery), except for removals.

One of the most commonly used catch-effort models for crustacean fisheries in eastern Canada is the Leslie model (Leslie and Davis, 1939). Braaten (1969) suggested enhancements to the Leslie model,

and a full description is presented in Ricker (1975). Recently, Gould and Pollock (1997) have shown that maximum likelihood estimation for q and u is more accurate and flexible. We used this method which consists of maximizing a multinomial likelihood function subject to the constraint $P_j = 1 - \exp(-qf_j)$. The variance of u is estimated via bootstrapping (see Gould and Pollock (1997) for further details). A visual assessment of the model validity is done by plotting the weekly values of CPUE against cumulative catches. The result should show a downward straight line, however a downward line does not assure the validity of the model.

2.4.2.2. Catch-effort model: open population: We have considered the model proposed by Paloheimo (1963). Estimates of M and q are obtained through the linear regression:

$$\log\left(\frac{CPUE_i}{CPUE_{i+1}}\right) = M + q\left(\frac{f_i + f_{i+1}}{2}\right), \quad i=1,2,\ t\text{-}1,$$

where f_i represent the effort during the interval (t_{i-1}, t_i). The model requires the assumptions I to IV listed above as well as:

i. M is constant, and is a Poisson process with regard to time.

2.4.3. CHANGE-IN-RATIO MODEL

In general, the CIR technique is the comparisons of relative abundance of two identifiable components from a population over time. Some authors (Udevitz and Pollock, 1995; Chen et al., 1998) have suggested modifications to the method. However, the new estimators developed require data not currently available from our lobster fisheries, and thus the modified methods were not considered. There are several variants to this technique (Paulik and Robson, 1969). In this paper, we applied the estimator to a population where only legal size lobsters are exploited. Estimated u is defined as:

$$\hat{u} = \frac{(p_1 - p_2)}{p_1(1 - p_2)},$$

where p_1 is the proportion of legal size animals in the first sample, and p_2 is the proportion of legal size animals in the second sample. The validity of the estimator relies on the following assumptions:

A. There is no migration, growth, or death.
B. All animals have the same probability of being capture in the i^{th} sample (i = 1, 2).

The variance of u was estimated by bootstrapping as described by Frusher et al. (1997).

2.4.4. COMPARISON OF RECAPTURE RATES

Independence of the probabilities of recapture with respect to the initial capture method, either trapping or SCUBA diving, was tested by a Chi-square test. No further analyses were done on tagged lobsters initially captured by SCUBA divers due to the small sample size.

2.4.5. SIMULATIONS

Simulations were used to assess the sensitivity of estimators u and M in cases where underlying assumptions are violated. For tagging and catch-effort models, observed fishery effort and total landings were used to generate possible weekly landings, and tag returns. Based on our knowledge of the fishery and the behavior of lobsters, we studied seven cases outlined in Table 3. It is known that a non constant (or variable) q is the most important cause of bias in the catch-effort model while tag loss, or unreported of tag recaptured (Hearn et al., 1998), is problematic with tagging models. For a spring lobster fishery, three factors can influence q: 1) at the beginning of the fishing season, the inshore lobster movement can result in a variable q, 2) the increase in water temperature will increase the lobster activity, thus q, and 3) the preparation for molting occurring at the very end of the fishing season can decrease q. In all the simulations but one, a generally accepted off-fishery annual natural mortality of 8% was used. To measure the estimators' sensibility to natural mortality, one case was simulated with a natural mortality set at 34%.

We simulated a fishery population of 100,000 lobsters, with effort equal to the weekly effort observed in Stonehaven during the 1997 fishery based on logbook data (Table 2). In addition, 289 and 355 tagged lobsters were also incorporated to the simulations to represent releases of tagged animals in September and May, respectively. For the tagged and unmarked animals, removal probabilities were generated as a product of conditional binomials, whereby a uniform random number was compared with the removal probability to determine the capture or non-capture of a particular animal. For animals tagged in September, an additional natural mortality representing the thirty-four weeks separating the release from the beginning of the fishery was also included. The removal probabilities were determined from a q and M input. An eight weeks fishery was simulated and landings, recapture of tagged animals, and the number of animals that died of natural mortality were collected, and used to compute simulated as well as calculated values of M and u. A simulation run consisted of 500 replications performed on S-PLUS (StatSci, 1995). Estimates of u and M were calculated for each run.

Simulations for the CIR technique were carried out separately because of different required parameters

mainly taken into account the calculations for sub-legal animals. Since all lobster traps are equipped with selective mechanisms allowing sub-legal lobsters to escape, q of these lobsters was allowed to be different from q of legal size animals in some cases (Table 4). Simulations correspond to the 1997 samplings done during the second and seventh week of the fishery. Starting with 100,000 legal size and 100,000 sub-legal animals, a simulated fishery took place for a week followed by a sampling during the second week. Legal size animals were removed while sub-legal animals were return to the population. No natural mortality was assumed for both groups of animals making the number of sub-legal animals constant at 100,000. The fishery then took place for six weeks after which another sample was taken. The simulated u and CIR estimate of u were calculated for the six weeks of the fishery covered by the study. These steps were repeated 500 times for all cases studied.

3.0. RESULTS

3.1. ESTIMATES BASED ON TAGGING AND FISHERY DATA

M-R estimates of u are equal to the proportion of tags returned whether the population is closed or open. However, variance estimators differ for the two models. In general, u estimates from M-R and M-M-R were lower than the ones from the catch-effort and CIR models (Table 5). For a closed population, estimates of the seasonal u were 31.5% and 36.6% for the September 1996 and May 1997 M-R, respectively (Table 5). Although the September 1996 M-R is based on the entire fishing season (eight weeks), and the May 1997 M-R includes only the last seven weeks of that season, the latter estimates of u are higher (Table 5). For an open population, the estimates of u were 31.5% and 22.4% for the September 1996 M-R and M-M-R, respectively (Table 5). The May 1997 open population M-R estimate of M was negative, hence all other estimates were rejected (Table 5). Estimates of M were 0.02 and 0.0057 for the September 1996 M-R and M-M-R, respectively (Table 5). Based on a forty-three (43) weeks off-fishing season, these estimates of 0.02 and 0.0057 represent an annual off-fishing season M of 58% and 22%, respectively.

Estimated value of u from the catch-effort model for a closed population was 68.8% (Table 5; Fig. 2). Assuming an open population, the catch-effort estimate of M was negative indicating that the method was inappropriate (Fig. 3). Thus, all other estimates were rejected (Table 5). Finally, the CIR estimate of u was the highest at 82.6%.

3.2. Comparison of recapture rates

The probabilities of recapture were not independent of the methods by which the animals were tagged. Probabilities of recapture of dive-tagged lobsters were significantly different from trap-tagged animals from September (Chi-square; $p = 0.01$) and May (Chi-square; $p = 0.006$) (Table 6). No dependence was observed between trap-tagged animals from the September and May tagging studies (Chi-square; $p = 0.17$).

3.3. Simulations

For each run of the simulations, a simulated u and estimated u from all models studied were calculated. The estimated u for all tagging models (September, May, and M-M-R) and three out of seven cases for the catch-effort models (closed and open population) were lower than the simulated values (Table 7). Furthermore, u from M-M-R were highly negatively biased (greater than 75%) for all simulated cases with calculated values ranging from 3% to 11%, while the simulated values varied between 31% to 66% (Table 7). Excluding case No 1 where the input M is higher (Table 3), u for the September 1996 M-R had a relatively low bias (Table 7). For the May 1997 M-R, the bias was higher. Furthermore, the only simulated case where the estimates of u were higher in May than September, as seen in field data (Table 5), required a high M input (case No 1, Table 7). For all other cases, u from September tagging was higher than the May tagging. The catch-effort model for a closed population tends to overestimate u (Table 7) for the cases considered suitable (cases No 1, 2, 3, and 7) for the model based on the diagnostic plots of CPUE against cumulative catch (Fig. 4). Cases No 4, 5, and 6 would have never been considered adequate for the catch-effort model for a closed population (Fig. 4). Finally, the catch-effort model for an open population provides an estimate of u only in cases No 1, 2, and 3 (Table 7). However for those cases, many of the 500 simulated runs resulted in a negative estimate for M and/or q, and were deleted from the calculations. Further, it was not possible to estimate u in cases No 4, 5, 6, and 7 (Table 7) because all estimates of q were negative. Cases No 4, 5, 6, and 7 would have never been considered adequate for the catch-effort model for an open population based on the diagnostic plots (Fig. 5).

The CIR simulations showed very little bias when catchability of legal and sub-legal animals is identical for a given sample (case a and b, Table 8) or catchability is different between groups but identical during both sampling (case d, Table 8). A substantial overestimation of u was observed when catchability varies both between studied groups and sampling periods (case c, Table 8).

As for u, estimators of M were studied via simulations. Except for the estimates of the catch-effort model and the M-M-R from case No 1, all other calculated estimates for M were extremely positively biased (Table 9).

4.0. DISCUSSION

Our simulations revealed weaknesses in all models studied. Departure from the model underlying assumptions resulted in bias of varying degrees depending on the method, and the parameters to be estimated. The M input had opposing effect on the estimates of u as it introduced a small (less than 7%) positive bias for the catch-effort model for a closed population, and a negative bias for the M-R model. The M-R from September could yield acceptable result if the M input was low (annual natural mortality around 10%) since results from simulations have shown that M greatly bias u estimated from the M-R model. Thus, tagging should be done as close as possible to the beginning of the fishery to avoid tag loss due to natural mortality or tag shedding. However, since we observed no recapture during the first week following the release of the lobsters tagged in May, there is evidence that tagged lobsters require time to recover from their tagging manipulation. Hence, an appropriate lapse of time of at least a week between the release of tagged animals and the recovery period is necessary.

Weekly variation in q also affected the estimates of u. For the M-R model, it tends to slightly affect the estimators. However, variations in q produced different biases depending on the nature of the variation for the catch-effort model for a closed population. If the weekly q decreased, u was overestimated. In a spring lobster fishery, q should decrease at the end of the fishing season in June since lobsters are entering the molting phase, and becoming less catchable. Conversely, an increase in weekly q produced an underestimate of u. However, diagnostic plots of CPUE against cumulative catch revealed that the catch-effort model was inappropriate. Graphical representations are essential tools in assessing a catch-effort model. Miller and Mohn (1993) had already warned against the validity of parameters estimated by the Leslie analysis, a catch-effort model using the least squares, for lobster and crab fisheries. Furthermore, they indicated that a decrease in q would result in a moderate to low bias. Our simulations have indicated the potential for a substantial bias.

The CIR estimator of u differs from the M-R and the catch-effort models as it incorporates data from the unexploited portion of the population. For this reason, q may differ between the legal and sub-legal animals, and/or between the two sampling periods. The technique assumes a different catchability between sampling periods, but identical q between groups at a given sampling period. Based on our simulations, different q between legal and sub-legal animals will not bias the estimate of u if q of both groups is constant for each sampling period. However, estimates of u were highly biased when q for each group was different between sampling periods.

Conversely to the estimates of u that were acceptable in some simulated cases, none of the method studied could adequately estimate M. We believe that a low value of M could explain the lack of accuracy of the methods. For instance, although simulated cases No 1 and 2 used the same parameter input, except for a lower M input in case No 2, the bias of M in case No 2 can reach up to twelve times the value of the bias in case No 1. Unless the natural mortality is suspected to be high, none of the methods studied is recommended to estimate the value of M.

The catch-effort model for an open population and M-M-R model are not adequate methods to estimate fishery parameters for lobster populations, and should not be used. These models use the estimate of M to derive an estimate for u, and since the estimate of M is unacceptable, the resulting u is highly biased.

Tagging data from May M-R redeemed higher estimates of u than the September M-R. This was unexpected since the estimates of u from May M-R were for a shorter fishing season than the September M-R. To obtain a similar pattern in the simulations, a high M input (over 35%) was required. We do not believe such a high value of M is the case in nature. However, tag loss (or tag-induced mortality) is equivalent to mortality, and could be a serious problem. A high tag loss for the September M-R, could explain the lower estimates. Unfortunately, information on streamer tag loss for lobsters are not available. Another explanation for the difference in u estimates could be the difference in the experimental design. Tagged lobsters were released at a single site in the September M-R compared to a random release over the fishing ground during the May M-R. The non-reporting of tagged lobsters recaptured by fishermen could also be a problem. However, since similar tags were used for both tagging projects, the difference in the tag-reporting rate should be negligible. Another possibility is the availability of lobsters over the fishing ground. It is known that lobsters in the GSL migrate from offshore to inshore in the spring (Corrivault, 1948; Munro and Therriault, 1983) during the lobster fishing season. Lobsters tagged in May were known to be on the fishing ground while some of the lobsters tagged in September might have still been absent from the fishing ground at least at the beginning of the recovery period (fishing season). However, solely the non-availability of certain tagged lobsters would not explain the discrepancy in u between the September and May M-R (see simulated case No 6).

Recapture rates of tagged lobsters seemed to be influenced by their first method of capture. Pollock et al. (1990) indicated that the probability of capture could depend on the animal's prior history of capture, i.e. tagged animals may have a lower (trap-shyness), or a higher (trap-addiction) capture probability than unmarked animals. Carothers (1973) referred to this

as a contagion of catchability implying that the behavior of an animal tends to be altered after its initial capture, i.e. an animal might be frightened or hurt during the initial capture, and will not likely enter another trap. Based on our May tagging, there is evidence of possible tagging trauma (Burkenroad, 1951) experienced by lobsters after being captured by traps, and a need for a recovery period before the beginning of the fishery. Although the number of lobster tagged after being captured by SCUBA diving is small, our findings from the May tagging, and the recapture rate for trap- versus dive-tagged animal support a trap-shy response for lobsters. Conversely to the trap-shy response that we observed, studies on the western rock lobster, *Panulirus cygnus* (Morgan, 1974), and the American lobster (Conan et al., 1984) showed that animals captured by traps, tagged, and released were more catchable than unmarked or dive-tagged animals. Conan et al. (1984) indicated that based on underwater video recordings, the difference in recapture rates was due to "clever" lobsters that can enter the trap, eat the bait, and walk out. As these lobsters can avoid being captured by trap, Conan et al. (1984) indicated that the probability of recapturing a tagged lobster previously captured by another method such as diving would be lower. Thus, trap-tagged lobsters do not have a similar behavior as dive-tagged animals. This raises some questions: do tagged and unmarked lobsters have the same catchability? Or, can estimates obtained from a tagged population be applied to the whole population? Trap response, either trap-shy or trap-addiction, is a source of bias, and should not be ignored if fishery parameters are to be estimated from tagging data based on trapping. To avoid the trap response, a different method of initial capture should be used.

The u estimate of 69% and 83% from the catch-effort model and the CIR technique, respectively, seem to better reflect the fishery reality than the 32% to 37% from M-R. In Stonehaven, very few large animals (> 81-mm CL) are observed in the catch, and lobsters in their first or second year into the fishery (67.5- to 81-mm CL) represent over 90% of the landings (Robichaud et al., 1996). Unless there is a large emigration, which is not supported by multi-year movement studies in that area (Comeau et al., 1999) or large lobsters are not catchable, size composition of the landings from Stonehaven would suggest a high fishing mortality. In addition, the fishing area is relatively small, homogeneous in its bottom type, and traps cover the entire fishing ground (no patchy fishing pattern). Also, fishermen use the same type and size of traps. Therefore, in this present study the underlying assumptions of the catch-effort and CIR models seem to be respected, except possibly for the constant q. However, the CIR estimate of 83% is the highest value of u for the shorter covered period. There is no obvious explanation for this, except a possible variable q of sub-legal lobsters.

The American lobster in eastern Canada is managed through large areas (LFA) with heterogeneous fishing strategies. We showed that even for a small area with homogenous characteristics the models studied are to be used with caution to estimate fishery parameters. Ennis et al. (1982) had similar results while estimating u and Z using both tagging studies and fishery data (catch and effort) between 1975 and 1980. They showed that using two different models on the same lobster fishery can give substantial different Z values, and indicated that the choice of the method and parameters used to estimate mortality should reflect the reality of the fishery being studied. Thus, models should not be suitable to manage entire LFA, unless perhaps a stratified approach is used. It is believed that the catch-effort (Lanteigne et al., 1998) or CIR model may be used in certain areas where underlying assumptions can possibly be met. Nevertheless, one of the major obstacles to estimate a sound lobster management plan is the lack of fishery independent surveys to verify parameter estimates produced by models. Such an approach has proven beneficial for the management of snow crab (*Chionoecetes opilio*) fisheries in the sGSL (Loch et al., 1995). Prior to 1988, the snow crab stock assessment relied entirely on estimates calculated by the widely criticized Leslie analysis (Miller and Mohn, 1993), and at the end estimates were regarded as unreliable to provide advice regarding a total allowable catch for conservation purposes (Loch et al., 1995). At that time, a post-fishery trawl survey was proposed in order to produce a fishery independent, and more accurate estimate of the biomass (Conan, 1985; Conan et al., 1988). This approach is still in place now (Hébert et al., 2000), and has proven to be a good management tool (Loch et al., 1995). Unfortunately, conversely to the U.S. where F for the lobster fishery can be derived from a modified DeLury model fit to sub-areas based on trawling surveys, trawling is not an acceptable tool to survey lobster in the sGSL. In sGSL, prime lobster habitat where intensive lobster fisheries are taken place is usually characterized by hard rocky bottom unsuitable for trawling. The development of an accurate stock assessment methodology is urged to estimate reliable fishery parameters by gathering a thorough knowledge of each LFA.

5.0. ACKNOWLEDGEMENTS

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Table 1. Exploitation rate (u) estimates for each Lobster Fishing Area (LFA) according to method of analysis. These u have been published by the Department of Fisheries and Oceans (DFO) in the Atlantic Fisheries Stock Status Report Series.

Year	LFA	u (%)	Method	Reference
1987-95	23	74.0	Catch curve	Anonymous (1996a)
1987-95	24	81.3		
1987-95	25	76.5		
1987-95	26A	78.0		
1987-95	26B	85.0		
1993	23	65.5	Leslie Analyses	
1994	23	68.7		
1995	23	61.6		
1993	24	78.0		
1994	24	79.8		
1955	24	84.6		
1993	26A	69.1		
1994	26A	57.0		
1995	26A	59.5		
1993	26B	76.9		
1994	26B	78.1		
1995	26B	72.5		
1996	27 (North-Central)	76.7	Leslie Analyses	Anonymous (1996b)
1996	27 (South)	49.0		
1996	30	34.0		
1993-94	27 (North-Central)	57.0*	Tagging	
1995	27 (South)	41.0*		
1993-95	27	50-69	Catch composition	
1993-94	29	47-55		
1993-96	30	3-55		
1986-95	31 (North)	20-47	Catch composition	Anonymous (1996c)
1986-95	31 (South)	45-59		
1986-95	32	47-66		
1986-94	33	60-80		
1983-92	34	73.0	Length cohort	Anonymous (1996d)
1993	34	73.0		
1994	34	75.2		
1995	34	71.0		

* These values represent the recapture rate from tagging studies.

Table 2. Weekly tag recovery, weekly landings (kg) and effort (trap haul) during the eight weeks of the 1997 American lobster (*Homarus americanus*) fishery in Stonehaven, New Brunswick. The recovery period started on 3 May, 1997.

Week	Number of tag recover (trap-tagged in 1996)	Number of tag recover (dive-tagged in 1996)	Number of tag recover (trap-tagged in 1997)	Landings (kg)	Effort (Number of trap haul)
1	10	1	-	3,774	6,355
2	9	5	7	3,417	6,520
3	20	8	23	3,500	7,050
4	13	0	32	2,452	5,973
5	16	0	34	2,096	6,117
6	12	1	18	1,600	5,568
7	8	4	13	1,119	5,450
8	3	0	3	574	2,772
total	91	19	130	18,532	45,805

Table 3. Parameters used for tagging and catch-effort simulations.

Case	Parameters
1	Fix catchability (q)=0.000024 and instantaneous natural mortality (M)=0.01, which represent an approximate off-fishery annual natural mortality of 34%.
2	Fix q=0.000024 and M=0.002, which represent an approximate off-fishery annual natural mortality of 8%.
3	Steady decrease of q from 0.000024 to 0.00001 by intervals of 2×10^{-6} and M=0.002.
4	Steady increase of q from 0.00001 to 0.000024 by intervals of 2×10^{-6} and M=0.002
5	Catchability (q) follows the proportion of weekly tag return, with values of 5.4×10^{-6}, 5×10^{-6}, 1.1×10^{-5}, 8.9×10^{-6}, 1.1×10^{-5}, 1.0×10^{-5}, 7.2×10^{-6}, 5.4×10^{-6}, and M=0.002.
6	Fix q=0.000024, M=0.002. Animals enter the fishery in three waves with 65%, 87%, and 100% availability during the first, second, and third week, respectively, followed by 100% availability until the end of the fishery. Not applicable for the May tagging since all tagged animals were considered available to the fishery from the beginning.
7	Catchability decreases from 0.000024 to 0.00001 by intervals of 2×10^{-6}, M=0.002. Animals enter the fishery in three waves as described in case No 6. Not applicable for the May tagging as per the reason given in case No 6.

Table 4. Parameters used for the change-in-ratio simulations.

Case	Parameters
a	All population available to the fishery; catchability of sub-legal (q_s)= catchability of legal (q_l)=2.4×10^{-5}.
b	All population available to the fishery; q_s=q_l, steady decrease from 2.4×10^{-5} to 1.0×10^{-5} by steps of 2×10^{-6}.
c	All population available to the fishery; q_s had a steady increase from 1.0×10^{-5} to 2.4×10^{-5} by steps of 2×10^{-6}, q_l had a steady decrease from 2.4×10^{-5} to 1.0×10^{-5} by steps of 2×10^{-6}.
d	All population available to the fishery; q_s=0.8×10^{-5}, q_l=2.4×10^{-5}.
e	Lobsters entering the fishery in waves with 65%, and 87% availability on the first, and second week, and 100% from the third week; q_s=q_l=2.4×10^{-5}.
f	Lobsters entering the fishery in waves with 65%, and 87% availability on the first, and second week, and 100% from the third week; q_s=q_l, steady decrease from 2.4×10^{-5} to 1.0×10^{-5} by steps of 2×10^{-6}.
g	Lobsters entering the fishery in waves with 65%, and 87% availability on the first, and second week, and 100% from the third week; q_s had a steady increase from 1.0×10^{-5} to 2.4×10^{-5} by steps of 2×10^{-6}, q_l had a steady decrease from 2.4×10^{-5} to 1.0×10^{-5} by steps of 2×10^{-6}.
h	Lobsters entering the fishery in waves with 65%, and 87% availability on the first, and second week, and 100% from the third week; q_s=0.8×10^{-5}, q_l=2.4×10^{-5}.

Table 5. Estimated fishing mortality ($\hat{F}$), natural mortality ($\hat{M}$) and exploitation rate ($\hat{u}$) from mark-recapture and catch-effort models for the 1997 American lobster (*Homarus americanus*) fishery in Stonehaven, New Brunswick. The confidence intervals are in parenthesis. Values and confidence intervals for $\hat{u}$ are in percentage.

Model	Method of estimation	Parameter (standard deviation) $\hat{F}$	$\hat{M}$	$\hat{u}$ (%)
Population	Mark-recapture, Sept. 96 [1]	0.047	-	31.5
				(28.2 , 34.8)
closed	Mark-recapture, May 97 [2]	0.065	-	36.6
				(33.4 , 39.8)
	Catch-effort model [1,3]	0.145	-	68.8
		(0.140 , 0,150)		(68.2 , 69.4)
	Change-in-ratio [3,4]	0.291		82.6
				(71.0 , 89.0)
Population	Mark-recapture, Sept. 96 [1]	0.052	0.02	31.5
		(-0.055, 0.159)	(-0.010 , 0.052)	(28.8 , 34.2)
open	Mark-recapture, May 97 [5]	n/a	n/a	n/a
	Mark-mark-recapture [6]	0.037	0.0057	22.4
		(-0.0008 , 0.0121)	(-0.030 , 0.104)	(4.2 , 40.6)
	Catch-effort model [5]	n/a	n/a	n/a

[1] Annual u is for a fishing season of eight weeks, $\hat{F}$ is calculated as $-\ln(1-\hat{u})/8$.

[2] Annual u is for a fishing season of seven weeks, $\hat{F}$ is calculated as $-\ln(1-\hat{u})/7$.

[3] Standard deviation estimates or the confidence interval were obtained from bootstrapping.

[4] Annual u is for a fishing season of six weeks, $\hat{F}$ is calculated as $-\ln(1-\hat{u})/6$.

[5] Estimates were not calculable for the fishery data set, yielding a negative M and q.

[6] Annual u is for a fishing season of seven weeks.

Table 6. Recapture rates of American lobster (*Homarus americanus*) by different sampling methods (SCUBA diving and trapping).

Date and initial sampling method	Number of lobster tagged	Number of lobster recaptured	Percentage of recapture
Sept. 96-SCUBA	36	19	52.8%
Sept. 96-traps	289	91	31.5%
May 97-traps	355	130	36.6%

Table 7. Average exploitation rate u, average relative bias in parenthesis, and 95% confidence interval from 500 simulations. Values are expressed in percentages. Cases are outlined in Table 3.

Case	Simulated u	Catch effort (close population)	Catch effort (open population)	September tagging	May tagging	combined tagging
1	64.76	69.06 (6.64)	56.10 (-17.46)*	45.95 (-29.05)	50.94 (-21.35)	8.94 (-86.19)
	(64.55 , 65.00)	(68.37 , 69.68)	(27.69 , 68.44)	(42.69 , 49.46)	(46.85, 54.83)	(7.79 , 9.93)
2	66.31	67.20 (1.35)	16.98 (-74.65)*	61.81 (-6.78)	52.36 (-21.03)	9.13 (-86.23)
	(66.04 , 66.55)	(66.44 , 67.91)	(13.81 , 19.25)	(57.68 , 65.9)	(48.33 , 56.94)	(8.06 , 10.02)
3	55.37	81.67 (47.51)	33.66 (-38.77)*	51.67 (-6.68)	41.55 (-24.96)	10.46 (-81.1)
	(55.11 , 55.62)	(81.19 , 82.14)	(3.701 , 64.32)	(47.22 , 56.49)	(36.78 , 46.12)	(9.67 , 11.11)
4	52.10	0.00 (-100)	**	48.47 (-6.96)	46.07 (-11.56)	2.66 (-95.1)
	(51.84 , 52.35)	(1.61E-08,1.96E-07)		(43.99 , 52.83)	(41.7 , 50.22)	(0.006 , 5.42)
5	31.20	1.28 (-95.9)	**	29.10 (-6.74)	27.77 (-11)	4.41 (-86.01)
	(30.97 , 31.44)	(1.44E-07 , 3.82)		(24.86 , 33.45)	(24.07 , 31.49)	(1.19 , 6.92)
6	63.56	44.46 (-30.05)	**	56.74 (-10.72)	50.16 (-21.09)	8.07 (-87.3)
	(63.32 , 63.81)	(43.37 , 45.58)		(52.21 , 60.71)	(46.09 , 54.16)	(6.82 , 9.19)
7	51.82	65.59 (26.59)	**	46.24 (-10.78)	39.62 (-23.54)	9.77 (-81.13)
	(51.57 , 52.08)	(64.81 , 66.33)		(41.45 , 50.37)	(35.37 , 43.92)	(8.91 , 10.54)

*: due to negative values of the estimates in certain runs, mean and standard deviation were replaced by median and interquartile range.

**: due to negative values for the catchability in case 4, 5, 6, and 7 for the catch-effort model for an open population, no u was estimated.

Table 8. Average exploitation rates (u), average relative bias in parenthesis, and 95% confidence interval from 500 simulations using the change-in-ratio estimator. Values are expressed in percentages.

Cases studies	Simulated u	Change-in-ratio
a	52.75	52.75 (0.003)
	(52.50 , 53.02)	(51.15 , 54.28)
b	43.31	43.31 (0.007)
	(43.02 , 43.58)	(41.01 , 45.56)
c	43.33	82.11 (89.5)
	(43.06 , 43.6)	(81.37 , 82.83)
d	52.74	52.31 (-0.82)
	(52.46 , 53.03)	(50.20 , 54.34)
e	51.59	50.93 (-1.29)
	(51.33 , 51.87)	(49.31 , 52.681)
f	42.08	41.16 (-2.2)
	(41.81 , 42.34)	(38.66 , 43.44)
g	42.07	81.46 (93.6)
	(41.81 , 42.33)	(80.7 , 82.2)
h	51.59	50.40 (-2.3)
	(51.33 , 51.88)	(48.29 , 52.74)

Table 9. Percentage of average weekly natural mortality rate ($\hat{M}$), average relative bias in parenthesis, and 95% confidence interval from 500 simulations, and the simulated natural mortality (M). Values are expressed in percentages. Cases are outlined in Table 3.

Case	Simulated M	Catch effort	September tagging	May tagging	Combined tagging
1	0.01	0.044 (363.2)* (0.0028 , 0.1173)	0.095 (889.76) (0.055 , 0.136)	0.087 (807.2) (0.0457 , 0.127)	0.016 (68.76) (0.0126 , 0.0194)
2	0.002	0.035 (1739.3)* (0.00483 , 0.118)	0.050 (2523.45) (0.0212 , 0.0789)	0.080 (4066.78) (0.0420 , 0.119)	0.008 (330.42) (0.00520 , 0.0115)
3	0.002	0.216 (11719)* (0.093 , 0.338)	0.120 (6461.72) (0.0184 , 0.160)	0.160 (8624.64) (0.111 , 0.208)	0.006 (245.46) (0.00194 , 0.0105)
4	0.002	**	0.009 (361.92) (0.000819 , 0.0323)	0.017 (717.01) (0.00195 , 0.0533)	0.012 (511.77) (0.00853 , 0.0166)
5	0.002	**	0.041 (1978.08)* (0.00508 , 0.0881)	0.076 (3737.96) (0.022 , 0.135)	0.012 (492.55) (0.0064 , 0.0176)
6	0.002	**	0.0293 (1539.44)* (0.00455 , 0.0582)	0.084 (4606.96) (0.0464 , 0.124)	0.010 (437.55) (0.00637 , 0.013)
7	0.002	**	0.091 (5176.58) (0.0512 , 0.130)	0.169 (9716.46) (0.123 , 0.218)	0.008 (384.44) (0.00396 , 0.0126)

*: due to negative values of the estimates in certain runs, mean and standard deviation were replaced by median and interquartile range.

**: due to negative values for the catchability in case 4, 5, 6, and 7 for the catch-effort model for an open population no exploitation rate was estimated.

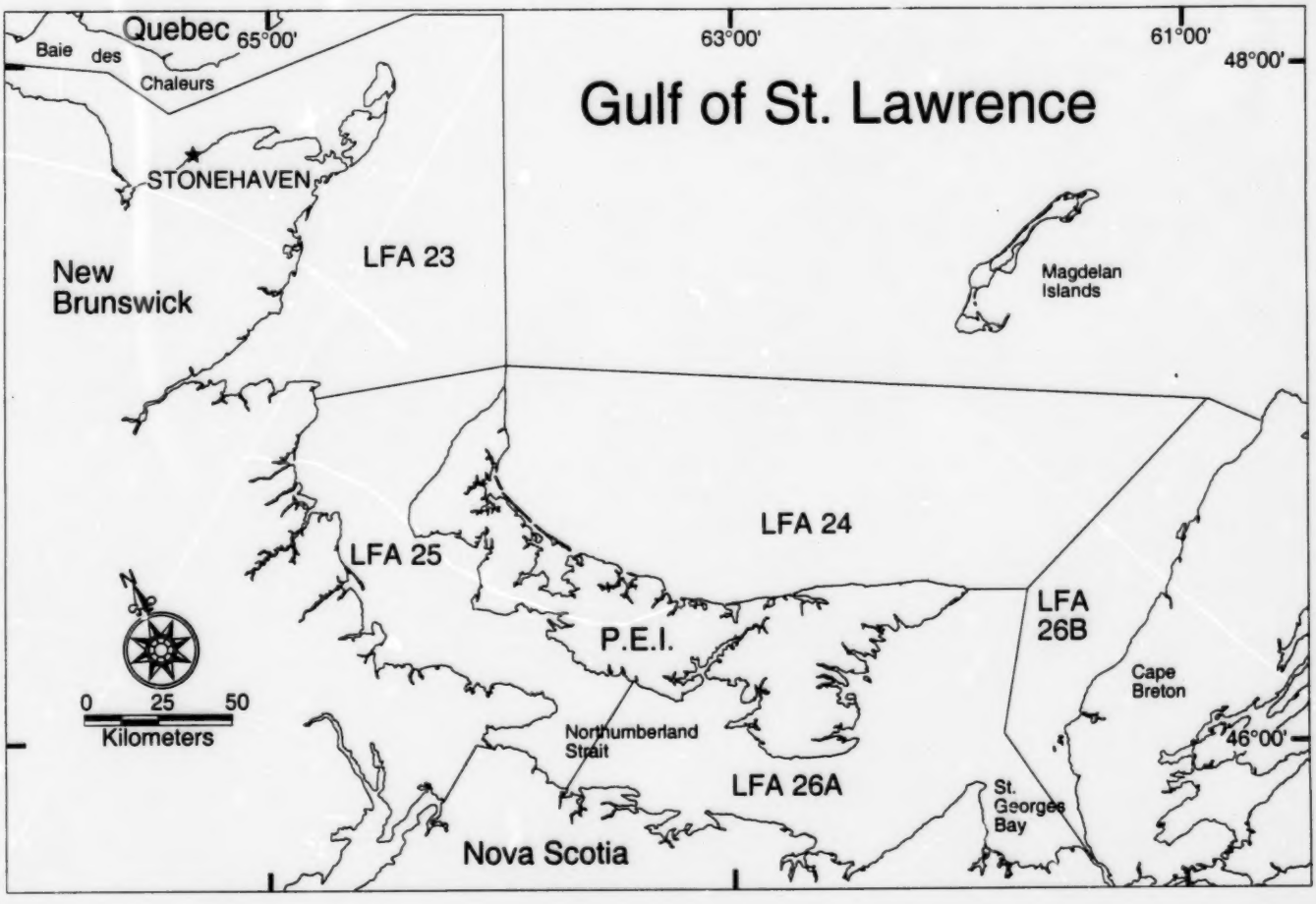

Figure 1. Location of the study site in Stonehaven New Brunswick. The Lobster Fishing Areas (LFA) are indicated on the map.

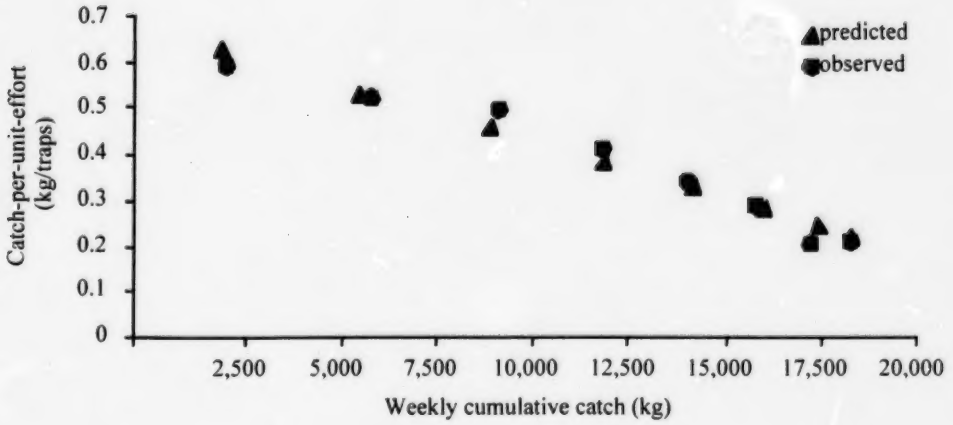

Figure 2. Weekly catch-per-unit-effort (CPUE) in relation to the weekly cumulative catch (kg).

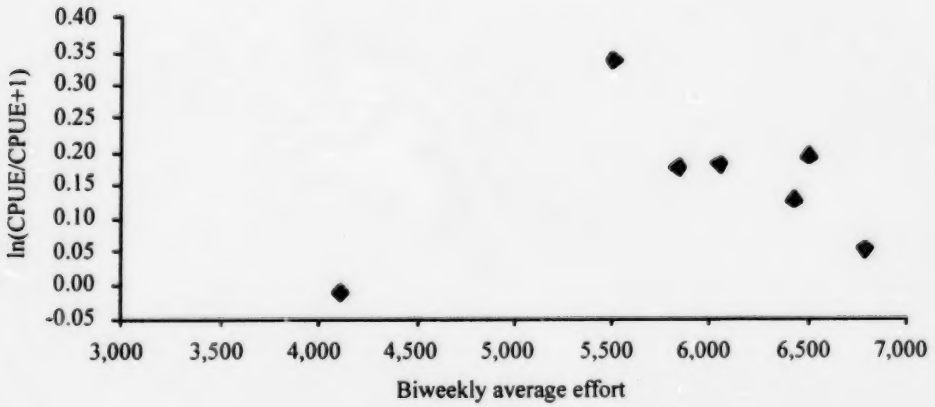

Figure 3. Log-transformed (ln) catch-per-unit-effort ($CPUE_i/CPUE_{i-1}$) in relation to the biweekly average effort (number of trap haul).

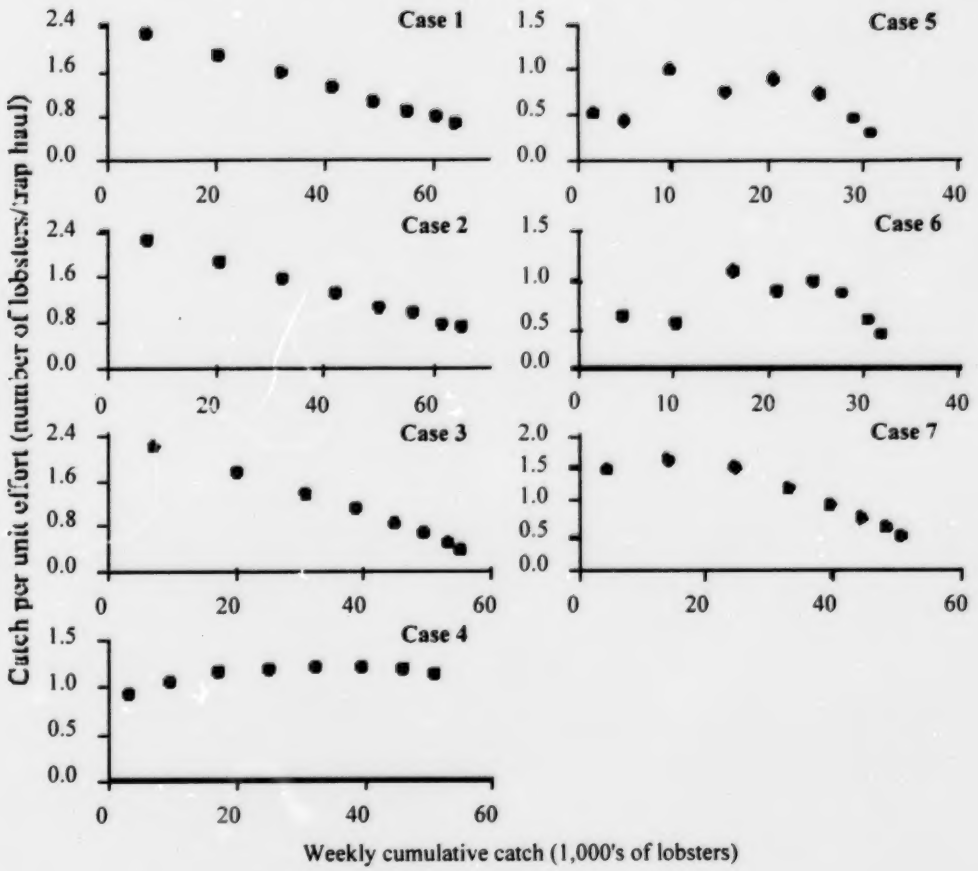

Figure 4. Weekly catch-per-unit-effort (CPUE) in relation to the cumulative catch (number of lobster) for the seven simulated cases.

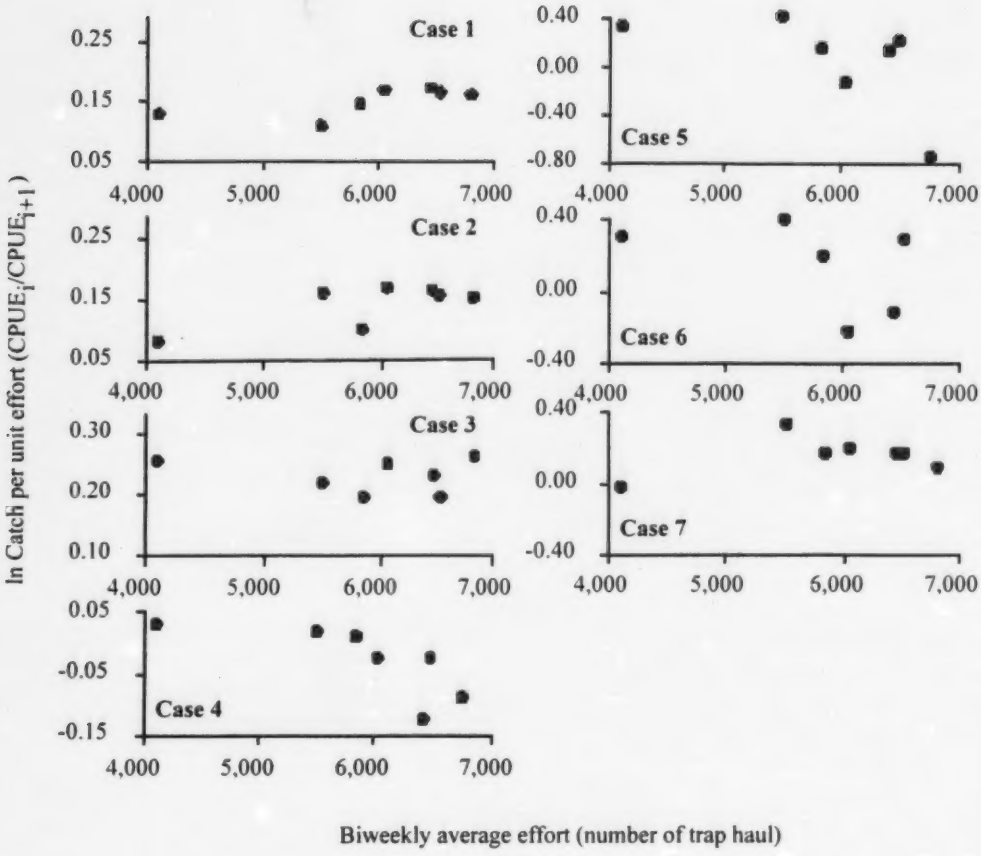

Figure 5. Log-transformed (ln) catch-per-unit-effort ($CPUE_t/CPUE_{t-1}$) in relation to the biweekly average effort (number of trap haul) for the seven simulated cases.

APPENDIX 1. MARK-RECAPTURE METHOD.

Suppose J periods of equal length denoted by $[0, d_1)$, $[d_1, d_2)$, ..., $[d_{J-1}, d_J)$, where $d_J=\tau$, the duration of the fishing season after which exploitation ceases, and that r_j tagged individuals are caught in the j^{th} interval (j=1, 2, ..., J), for a total of $r = \sum_{j=1}^{J} r_j$ recaptured individuals. Furthermore, let $Z = F + M$ be the total instantaneous mortality. The maximum likelihood estimates of the exploitation rate u_τ for the total fishing period τ is:

$$\hat{u} = \frac{\sum_{j=1}^{J} r_j}{m}$$

where m is the number of tagged individuals, and the total instantaneous mortality rate estimate $\hat{Z}$ is the solution of

$$\frac{\left(\sum_{j=0}^{J-1} j\exp\left(-\hat{Z}j\right)\right)}{\left(\sum_{j=0}^{J-1}\exp\left(-\hat{Z}j\right)\right)} = \frac{\sum_{j=1}^{J}(j-1)r_j}{r}.$$

The estimate of the instantaneous fishing mortality F per sampling period is:

$$\hat{F} = \frac{\hat{u}\hat{Z}}{(1-\exp(-\hat{Z}J))}$$

and $\hat{M} = \hat{Z} - \hat{F}$.
Asymptotic variance estimators are given by:

$$v(\hat{u}) = \frac{\hat{u}(1-\hat{u})}{m},$$

$$v(\hat{Z}) = \frac{1}{m\hat{u}}\left\{\frac{\exp(-\hat{Z})}{\left[1-\exp(-\hat{Z})\right]^2} - \frac{J^2\exp(-\hat{Z}J)}{\left[1-\exp(-\hat{Z}J)\right]^2}\right\}^{-1},$$

$$v(\hat{F}) = \hat{F}^2\left\{\frac{v(\hat{u})}{(\hat{u})^2} + \left[1 - \frac{J\hat{F}\exp(-\hat{Z}J)}{\hat{u}}\right]^2\frac{v(\hat{Z})}{\hat{Z}^2}\right\}$$

and

$$v(\hat{M}) = \hat{F}^2\left\{\frac{v(\hat{u})}{\hat{u}^2} + \frac{v(\hat{Z})}{\hat{Z}^2}\left[\frac{J\hat{F}\exp(-\hat{Z}J)}{\hat{u}} + \frac{\hat{M}}{\hat{F}}\right]^2\right\}.$$

APPENDIX 2. MARK-MARK-RECAPTURE METHOD.

Suppose there are J recovery periods of equal length denoted by $[0, d_1)$, $[d_1, d_2)$, ..., $[d_{J-1}, d_J)$, where $d_J=\tau$, the duration of the fishing season after which exploitation ceases, and that r_{ij} represents the number of tagged individuals from the i^{th} release that are caught in the j^{th} interval ($j=1, 2, ..., J$),. Let r_1 and r_2 be the total number of individuals recaptured from releases 1 and 2 respectively, with $r_{i.} = \sum_{j=1}^{J} r_{ij}$ and $r = r_1 + r_2$ is the combined number of individuals recaptured from both tagging releases. The maximum likelihood estimates of u_J, M, F and Z are:

$$\hat{u} = \frac{\hat{F}(1-\exp(-\hat{Z}J))}{\hat{Z}},$$

$$\hat{M} = \frac{1}{\tau_1}\ln\left(\frac{r_2 m_1}{r_1 m_2}\right),$$

$$\hat{F} = \hat{Z} - \hat{M}$$

and $\hat{Z}$ is the solution of

$$\frac{\sum_{j=0}^{J-1} j\exp(-\hat{Z}j)}{\sum_{j=0}^{J-1}\exp(-\hat{Z}j)} = \frac{\sum_{j=1}^{J}\left[(j-1)\left(\sum_{i=1}^{2} r_{ij}\right)\right]}{r}.$$

The tag-induced mortality can be estimated as $\hat{c} = r_2\left(m_2\hat{u}\right)^{-1}$.

Approximate variances estimators are given by:

$$v(\hat{Z}) = \left\{ r\left[\frac{\exp(-\hat{Z})}{\left[1-\exp(-\hat{Z})\right]^2} - \frac{J^2\exp(-\hat{Z}J)}{\left[1-\exp(-\hat{Z}J)\right]^2}\right]\right\}^{-1},$$

$$v(\hat{M}) = \frac{1}{(\tau_1)^2}\left[\frac{m_1 - r_1}{m_1 r_1} + \frac{m_2 - r_2}{m_2 r_2}\right],$$

$$v(\hat{F}) = v(\hat{Z}) + v(\hat{M})$$

and

$$v(\hat{u}) = \hat{u}^2\left\{\frac{v(\hat{M})}{\hat{F}^2} + \frac{v(\hat{Z})}{\hat{Z}^2}\left[\frac{J\hat{F}\exp(-\hat{Z}J)}{\hat{u}} + \frac{\hat{M}}{\hat{F}}\right]^2\right\}.$$